

Production Ecology of the Seagrass *Zostera marina* in Jindong Bay, Korea

Kun-Seop Lee*, Jung-Im Park, Ik Kyo Chung¹, Dong Woo Kang¹ and Sung-Hoi Huh²

Department of Biology, ¹Department of Marine Science, Pusan National University, Busan 609-735 and

²Department of Oceanography, Pukyong National University, Busan 608-737, Korea

Production dynamics of eelgrass, *Zostera marina* was examined in Jindong Bay on the south coast of the Korean peninsula. Eelgrass leaf productivities and environmental factors such as underwater photon flux density, water temperature, and nutrient availabilities in the water column and sediments were monitored from March 2002 to December 2003. While water temperature exhibited a distinct seasonal trend, underwater irradiance and nutrient availabilities exhibited high degree of fluctuation, and did not show a seasonal trend throughout the experimental periods. Eelgrass leaf elongation and production rates showed significant seasonal variations. Leaf productivity was highest in May (30.0 mg dry wt sht⁻¹ d⁻¹ or 3.7 g dry wt m⁻² d⁻¹) and lowest in November (3.2 mg dry wt sht⁻¹ d⁻¹ or 0.12 g dry wt m⁻² d⁻¹). Eelgrass leaf productivities did not show a strong correlation with underwater irradiance or environmental nutrient availabilities. The production rates, however, were positively correlated with water temperature during spring periods, and were correlated negatively at high water temperature exceeded 20°C during summer months. While relative growth rates were highest in spring and lowest in high water temperature periods, plastochrone interval was longest during summer and shortest during spring. These results imply that seasonal growth dynamics of eelgrass, *Z. marina* was mainly controlled by water temperature.

Key Words: productivity, seasonal variation, seagrass, underwater irradiance, water temperature, *Zostera marina*

INTRODUCTION

Seagrass habitat is an important component of estuarine and coastal ecosystems and is one of the most productive plant communities of the world (McRoy and McMillan 1977, Zieman and Wetzel 1980). Seagrasses influence the immediate abiotic environment by enhancing sedimentation and sediment binding, reducing current and wave velocities and acting as a nutrient filter (Ward *et al.* 1984; Fonseca 1989; Lee and Dunton 1999). Seagrasses also provide essential three-dimensional habitats for a wide variety of marine animals and plants and are a source of organic carbon for economically important animals (Heck and Westone 1977; Orth *et al.* 1984; Summerson and Peterson 1984; Huh and Kitting 1985). Although few herbivores consume seagrasses directly (Ogden 1980; Mann 1988), a substantial fraction of seagrass carbon enters coastal and estuarine food webs through microbial transformation of litter and particulate detritus (Kenworthy and Thayer

1984; Mann 1988; Chin-Leo and Benner 1991; Koepfler *et al.* 1993, Opsahl and Benner 1993; Peduzzi and Herndl 1991).

Primary productivity of seagrasses is mainly regulated by variations in underwater photon flux density, water temperature, and environmental nutrient availabilities (Phillips *et al.* 1983; Wetzel and Penhale 1983; Dunton 1994). Underwater light has been considered as a major factor controlling seagrass growth and distribution (Wetzel and Penhale 1983; Dennison 1987; Dennison *et al.* 1993; Lee and Dunton 1997). Seagrasses require light for photosynthesis, therefore their growth, survival and depth distribution are directly related to light availability (Dennison *et al.* 1993). Large losses of seagrass areal coverage have been reported as a consequence of decreased underwater light availability (Cambridge and McComb 1984; Giesen *et al.* 1990; Dennison *et al.* 1993; Onuf 1994). Underwater light reduction caused by epiphytic and planktonic algal blooms due to input of excess anthropogenic nutrients, increased sediment runoff, resuspension of bottom sediments and dredging have been linked to the declines of seagrass productivity and coverage in many parts of the world (Orth and

*Corresponding author (klee@pusan.ac.kr)

Moore 1983; Cambridge *et al.* 1986; Onuf 1994; Czerny and Dunton 1995; Lee and Dunton 1997).

Although underwater irradiance largely regulates primary productivities of seagrasses, seasonal trends of seagrass leaf productivities did not strongly correlated with photon flux density (Lee and Dunton 1996). Seagrass leaf productivity usually shows clear seasonal trends with rates increasing during spring and summer and decreasing during fall and winter (Vermaat *et al.* 1987; Dunton 1994; Lee and Dunton 1996). Since temperature significantly affects the biochemical process involved in photosynthesis and plant tissue metabolism, water temperature has been considered as a major factor controlling seagrass seasonal growth (Tutin 1942; Phillips *et al.* 1983; Lee and Dunton 1996; Lee *et al.* 2003). Strong correlation between seagrass leaf productivities and water temperature has been reported for the tropical seagrass species, *Thalassia testudinum* (Lee and Dunton 1996). However, temperate seagrass species, *Zostera marina* showed different seasonal trends from that of the tropical seagrass species (Lee *et al.* 2003). In the present study, we examined in detail temperature effects on primary productivities of the temperate seagrass, *Zostera marina*.

Endogenous circannual rhythms of leaf production have been suggested for the several seagrass species (Ott 1979; Dunton 1994; Czerny and Dunton 1995). Onset of rapid leaf growth of *Halodule wrightii* every May has been observed regardless of environmental light conditions, suggesting existence of endogenous circannual rhythms for seagrass leaf growth (Dunton 1994). In the present study, leaf productivities in relation to coincident measurements of underwater photon flux density, water temperature and sediment and water column nutrient availabilities were monitored to examine seasonal growth dynamics of seagrass *Zostera marina* in the bay system of the south coast of the Korean peninsula.

MATERIALS AND METHODS

Study site

The study site is located in Jindong Bay on the south coast of the Korean peninsula (Fig. 1). The study was conducted on a monotypic *Zostera marina* bed with an average water depth of about 3m. Sediments in the bed consist of about 20% sand, 20% clay and 60% silt. Seagrass leaf production and physico-chemical parameters such as underwater photon flux density,

water temperature, sediment and water column nutrient availabilities of the study site were monitored from March 2002 to December 2003.

Leaf productivity measurements

Leaf productivities were measured using the modified leaf marking technique (Zieman 1974; Kentula and McIntire 1986; Lee and Dunton 1996). About 10 randomly chosen eelgrass shoots were punched the bundle sheath with a hypodermic needle and then collected after 2 to 5 weeks. Separated leaf materials into leaf tissues produced before and after punching were measured lengths and widths and then dried at 60°C to a constant weight. The leaf productivity per shoot (g dry wt shoot⁻¹ d⁻¹) was determined by dividing the dry weight of new leaf tissue produced after punching by the number of the days since marking. Areal leaf productivity (g dry wt m⁻² d⁻¹) was obtained by multiplying shoot leaf productivity by the shoot density. Leaf elongation rates were determined by dividing total length of newly produced leaf tissues after marking by the number of experimental days. Relative growth rate (g dry wt g⁻¹ d⁻¹) and leaf turn-over time (d) were calculated with dry weights of newly produced leaf tissues and total leaf tissues. All newly emerged leaves after marking were counted for determination of the plastochrone interval of leaf. Plastochrone intervals were

calculated by dividing the time interval (days) between marking and collecting by the number of newly emerged leaves after marking.

Water temperature and underwater irradiance

Water temperature and underwater photon flux density were measured using Hobo data logger (Onset Computer Corp.) encased in a waterproof underwater housing every 15 min during the experimental periods. Measured water temperatures were averaged daily. Light intensity (lumens ft^{-2}) measured using Hobo data logger was converted to photon flux density ($\mu\text{mol photons m}^{-2} \text{sec}^{-1}$) by concurrent quantum measurements using an LI-1400 data logger and an LI-193SA spherical quantum sensor (LI-COR, Inc.). Daily photon flux density ($\text{mol m}^{-2} \text{d}^{-1}$) was calculated as the summation of quantum flux over each 24h period.

Water column and sediment nutrient availability measurements

Four replicate surface water samples were collected for determination of water column nutrient availability every month. Dissolved inorganic nitrogen (DIN, NH_4^+ , $\text{NO}_3^- + \text{NO}_2^-$), and PO_4^{3-} concentrations were determined colorimetrically according to Parsons *et al.* (1984). Concentrations of $\text{NO}_3^- + \text{NO}_2^-$ were determined after running through a column containing copper coated cadmium, which reduces NO_3^- to NO_2^- . Six to ten replicate sediment samples were collected randomly to a sediment depth of about 13cm with a syringe corer for determination of sediment nutrient availability. Samples were placed on ice and frozen pending lab analyses. Sediment pore water was obtained by centrifugation ($5000 \times g$ for 15min) and used for determination of pore water DIN and PO_4^{3-} concentrations. Concentrations of pore water DIN and PO_4^{3-} were determined after dilution (1:5; v/v) with low nutrient seawater. To determine sediment organic content, oven-dried sediments were burned at 550°C for 2h, and sediment organic content was calculated from the loss of sediment weight. Shells were removed from the sediments before combustion.

Statistics

All values are reported as means \pm 1SE. Statistical analyses were performed on a microcomputer using a general linear model procedure (SAS). Data were tested for normality and homogeneity of variance to meet the assumptions of parametric statistics. Differences in eelgrass leaf productivities and water column and pore

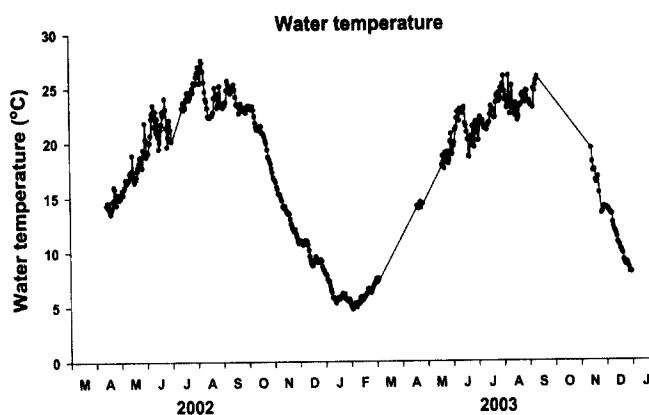


Fig. 2. Seasonal variation of water temperature at the study site in Jindong Bay.

water nutrient concentrations among sampling time were tested for significance using a one-way ANOVA. When a significant difference among variables was observed, the means were analyzed by a Tukey multiple comparison test to determine where the significant differences occurred among variables.

RESULTS

Water temperature and underwater photon flux density

Water temperature at the study site showed a strong seasonal trend ranging from 4.7°C in late January 2002 to 27.5°C in August 2002 (Fig. 2). However, underwater photon flux density, which was collected on a continuous basis, exhibited a high degree of fluctuation (Fig. 3). Monthly average daily photon flux density ranged from $2.1 \text{ mol photons m}^{-2} \text{d}^{-1}$ in July 2003 to $13.4 \text{ mol photons m}^{-2} \text{d}^{-1}$ in April 2002 (Fig. 3A). Daily maximal photon flux density exhibited a similar fluctuation pattern to that of daily photon flux density, and did not show a seasonal trend (Fig. 3B). Daily maximal photon flux density reached to about 2000 ($\text{mol photon m}^{-2} \text{s}^{-1}$) during April and November 2002.

Water column and sediment nutrient concentrations

Water column NH_4^+ concentrations varied significantly ($P < 0.001$) with sampling time, but did not show any distinct seasonal trend (Fig. 4A). Water column NH_4^+ concentrations were usually less than $3 \mu\text{M}$ during the study period. Water column $\text{NO}_3^- + \text{NO}_2^-$ concentrations also showed significant ($P < 0.001$) temporal variation, but not distinct seasonal trend (Fig. 4B). The concentrations were usually less than $5 \mu\text{M}$, except after the rain in April 2003. Water column PO_4^{3-}

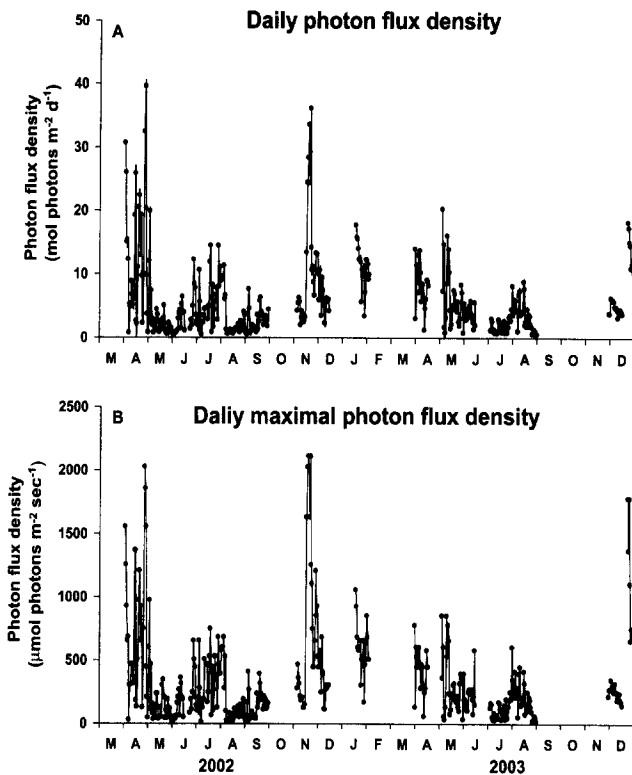


Fig. 3. Daily photon flux density and daily maximal photon flux density at the canopy level in a *Zostera marina* bed in Jindong Bay from April 2002 to December 2003.

concentrations significantly ($P < 0.001$) fluctuated with sampling time, but also did not show any clear seasonal trend (Fig. 4C). Phosphate concentrations in the water column were less than $1 \mu\text{M}$ in most cases.

Sediment pore water NH_4^+ concentrations were usually less than $200 \mu\text{M}$, but the concentrations reached to more than $500 \mu\text{M}$ after dredging event in the vicinity of the study site in June and July 2003 (Fig. 5A). Sediment pore water NH_4^+ concentrations varied significantly ($P < 0.001$) with sampling time, but did not show any seasonal trend. Sediment pore water $\text{NO}_3^- + \text{NO}_2^-$ and PO_4^{3-} concentrations also showed no obvious seasonal trend (Fig. 5B, C). Average sediment pore water $\text{NO}_3^- + \text{NO}_2^-$ and PO_4^{3-} concentrations were about $2 \mu\text{M}$ and $30 \mu\text{M}$, respectively. Sediment organic content varied significantly ($P < 0.001$) with sampling time, but also did not show constant seasonal trend (Fig. 5D). Average sediment organic content was about 7% in the study site.

Eelgrass leaf growth rates and plastochrone interval

Leaf elongation rates showed significant ($P < 0.001$) seasonal variation, increasing during spring and decreasing during summer and fall (Fig. 6). While leaf

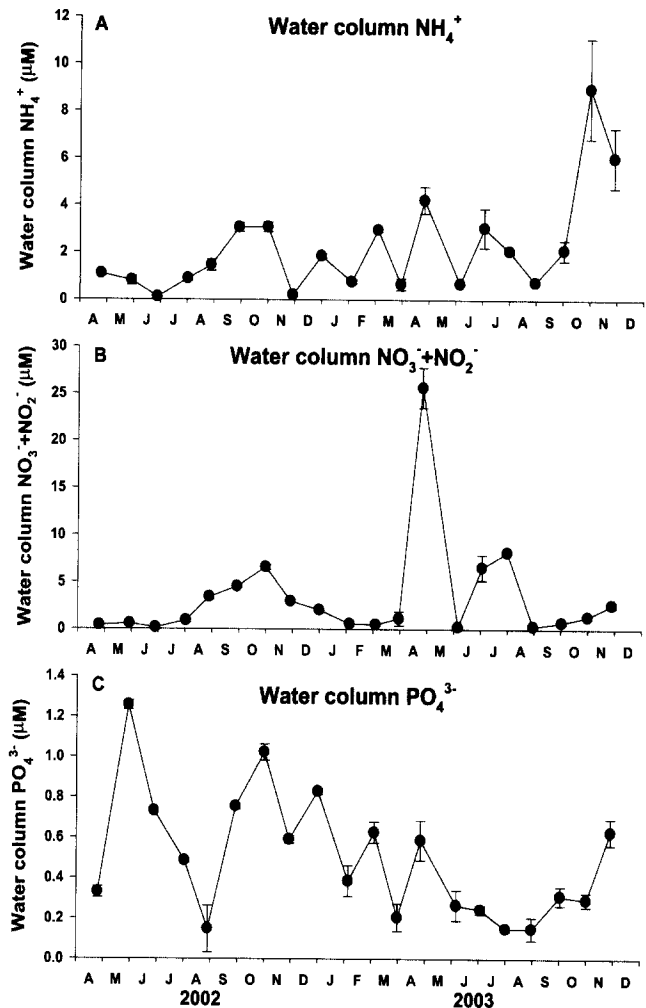


Fig. 4. Water column nutrient concentrations at the study site in Jindong Bay from April 2002 to December 2003. Values are mean \pm SE ($n = 4$).

elongation rates ranged from $1.7 \text{ cm leaf sht}^{-1} \text{ d}^{-1}$ in September 2002 to $10.6 \text{ cm leaf sht}^{-1} \text{ d}^{-1}$ in April 2002 on a eelgrass shoot basis (Fig. 6A), the rates on an areal basis ranged from $0.9 \text{ m leaf m}^{-2} \text{ d}^{-1}$ in November 2003 to $12.6 \text{ m leaf m}^{-2} \text{ d}^{-1}$ in early May 2002 (Fig. 6B). Eelgrass leaf productivities exhibited similar seasonal trend to that of leaf elongation rates (Fig. 7). Leaf productivities were highest during May ($30.0 \text{ mg dry wt sht}^{-1} \text{ d}^{-1}$ or $3.7 \text{ g dry wt m}^{-2} \text{ d}^{-1}$) and lowest in November ($3.2 \text{ mg dry wt sht}^{-1} \text{ d}^{-1}$ or $0.12 \text{ g dry wt m}^{-2} \text{ d}^{-1}$). While eelgrass leaf productivity was positively correlated with water temperature during spring months, the productivity was negatively correlated with water temperature during summer (Fig. 8). During fall and winter, however, there was not a strong correlation between leaf productivity and water temperature (Fig. 8).

Relative growth rates of eelgrass leaf tissues exhibited

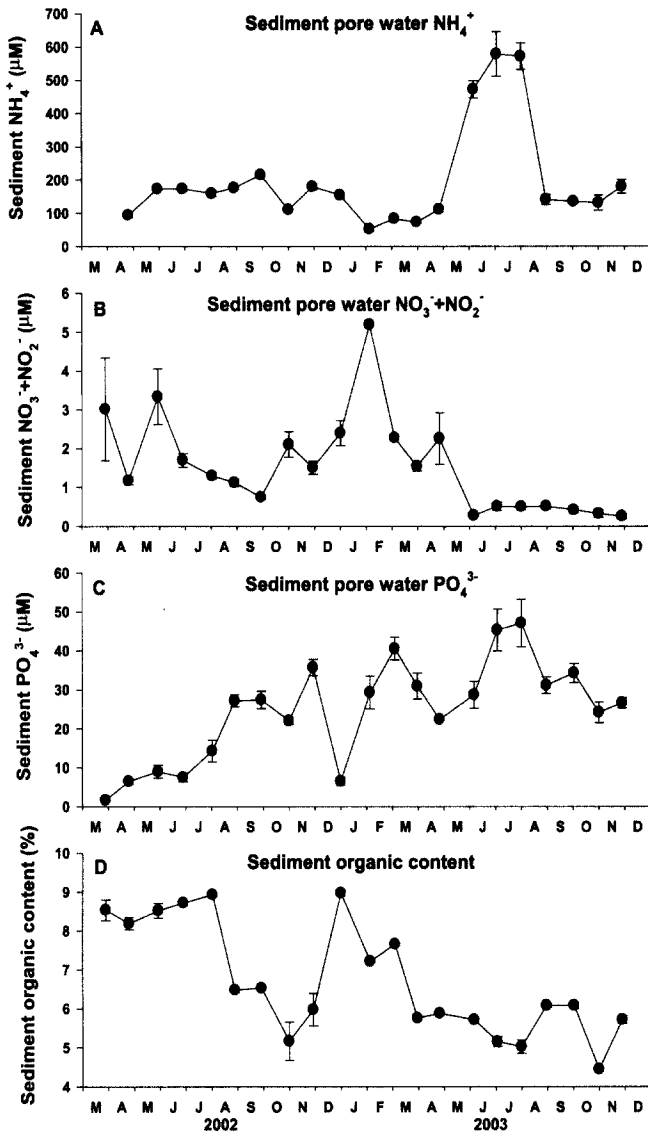


Fig. 5. Sediment pore water nutrient concentrations and sediment organic content at the study site in Jindong Bay from March 2002 to November 2003.

significant ($P < 0.001$) seasonal variations (Fig. 9A). Relative growth rates were lowest in June ($0.008 \text{ g new leaf g}^{-1} \text{ dry wt d}^{-1}$) and highest in April 2002 and March 2003 ($0.03 \text{ g new leaf g}^{-1} \text{ dry wt d}^{-1}$). Leaf turn-over time also showed significant ($P < 0.001$) seasonal variation, but reverse trend of the relative growth rates (Fig. 9B). Leaf turn-over time was longest in June 2002 (146.4 days) and shortest in March (34.2 days). Plastochrone interval of eelgrass leaf changed significantly ($P < 0.001$) with sampling time (Fig. 10). The interval was longer during summer and winter months than during spring and fall.

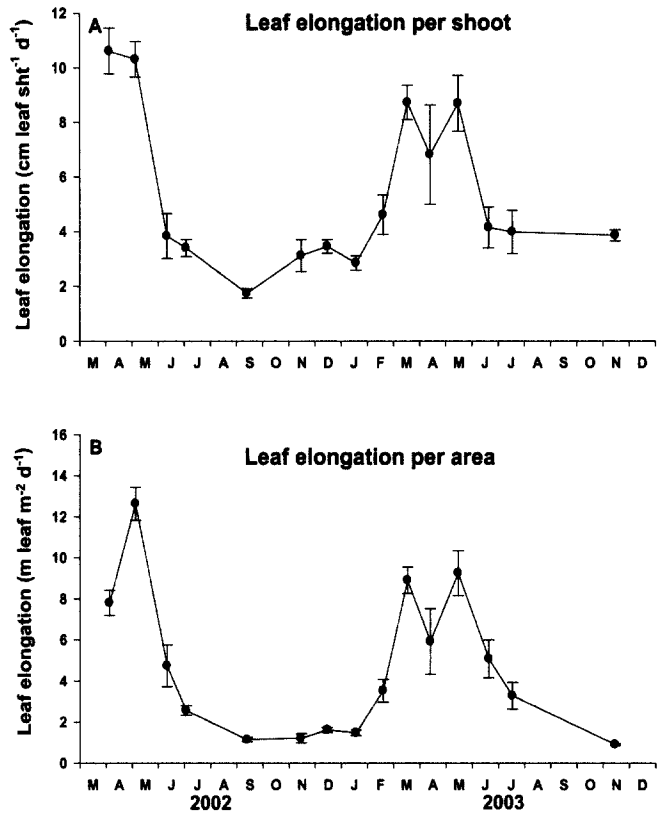


Fig. 6. Seasonal changes in leaf elongation rates of the eelgrass, *Zostera marina* from March 2002 to November 2003.

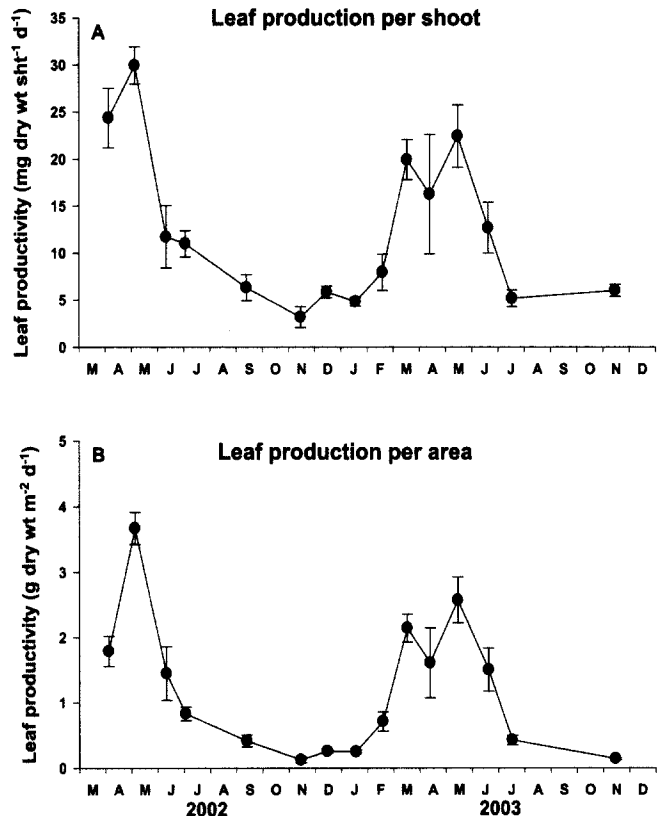


Fig. 7. Seasonal changes in eelgrass leaf productivities from April 2002 to November 2003.

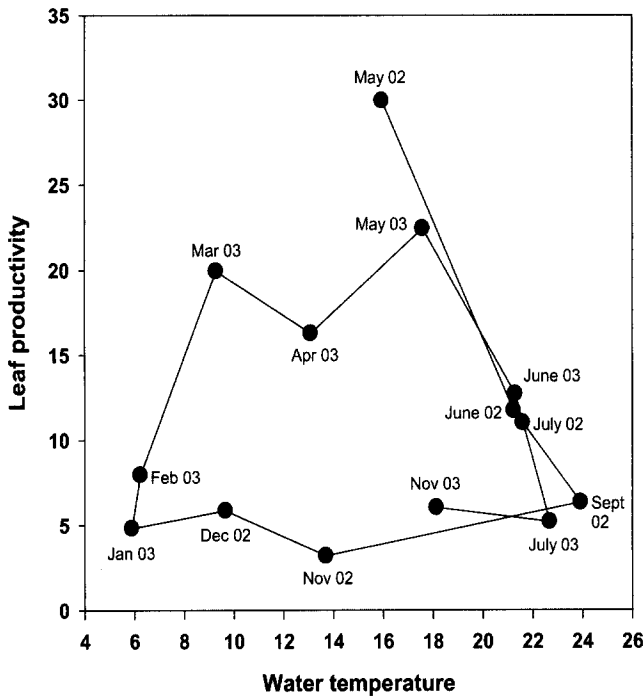


Fig. 8. Relationship between eelgrass leaf productivity and water temperature from May 2002 to November 2003.

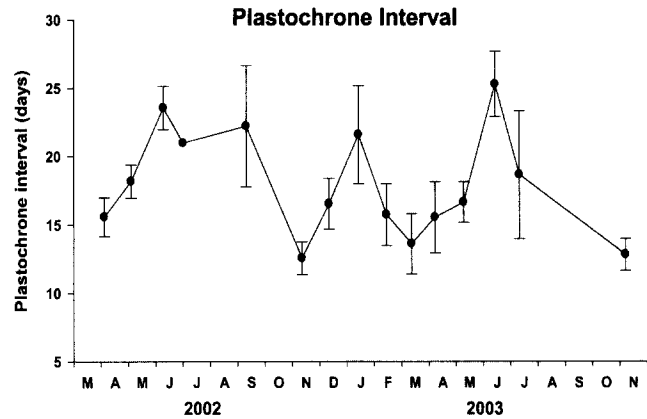


Fig. 10. Seasonal changes in leaf plastochrone interval of the eelgrass, *Zostera marina* from April 2002 to November 2003.

DISCUSSION

Since seagrass communities contribute significantly to the primary production of coastal and estuarine ecosystems, production dynamics of seagrasses has been a main subject of the seagrass researches (McRoy and McMillan 1977; Zieman and Wetzel 1980; Dunton 1990; Lee and Dunton 1996). Seagrass primary productivities are regulated by underwater irradiance, water temperature, and nutrient availabilities in the water column and sediment (Wetzel and Penhale 1983; Dunton 1994; Lee and Dunton 2000). Thus, variations in these factors are reflected in survival, distribution and temporal or special production variations of seagrasses. In the present study, productivities of eelgrass, *Zostera marina* exhibited distinct seasonal trend, increasing during early spring and decreasing during summer periods. This eelgrass growth trend, however, was not identical with the seasonal patterns of underwater irradiance, water temperature or nutrient availabilities.

Because seagrasses show high productivities, seagrasses require large amounts of inorganic nutrients for growth. Therefore, nutrient availability may play a significant role in controlling productions of seagrasses (Kenworthy *et al.* 1982; Romero *et al.* 1994; Lee and Dunton 2000). Nutrient enrichment studies have shown that seagrass growths were limited by environmental nutrient availabilities in many seagrass beds (Orth 1977; Harlin and Thorne-Miller 1981; Iizumi *et al.* 1982; Dennison *et al.* 1987; Short *et al.* 1990; Perez *et al.* 1991; Murray *et al.* 1992; Williams and Ruckelshaus 1993; Lee and Dunton 2000). In contrast to terrestrial plants, seagrasses can take up inorganic nutrients through leaf and root tissues from the water column and sediments (Iizumi and Hattori

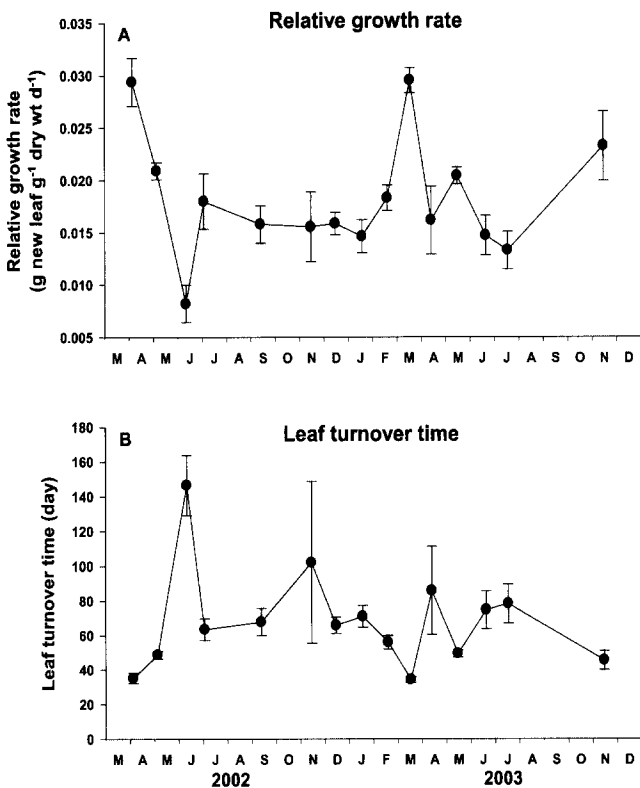


Fig. 9. Seasonal changes in relative growth rate and leaf turnover time of the eelgrass, *Zostera marina* from April 2002 to November 2003.

1982; Thursby and Harlin 1982, 1984; Short and McRoy 1984; Stapel *et al.* 1996; Pedersen *et al.* 1997; Terrados and Williams 1997; Lee and Dunton 1999). Inorganic nutrient in the water column and sediment pore water contributed equally to the nutrient budget of seagrass (Lee and Dunton 1999). In the present study, nutrient availabilities in the water column and sediment pore water were highly fluctuated, and did not show any distinct seasonal trends. Raining and human activity such as dredging events had significantly influences on the nutrient concentrations of the study site. Thus, environmental nutrient availabilities probably had no effect on the seasonal variations of the eelgrass growth. Variations in environmental nutrient availabilities may be reflected in the special variation of the seagrass production (Short 1983; Lee and Dunton 2000).

Seagrasses need to receive sufficient light for photosynthesis, and their survival, distribution, and growth are directly related to underwater light availability (Dennison *et al.* 1993). Underwater photon flux density in this study site highly fluctuated, but did not exhibit a seasonal trend. Underwater irradiance in the tropical seagrass beds also showed high fluctuation, but no seasonal trend (Lee and Dunton 1996). Since, underwater light intensity results from combinations of surface irradiance, water clarity, depth, and weather conditions, the intensity could fluctuate with no seasonal trend. Even underwater irradiance has an important effect on seagrass photosynthesis, consequently seagrass growth, seasonal trend of eelgrass growth did not appear to reflect variation in underwater irradiance. Underwater irradiance may have primary effects on survival and distribution of seagrass in certain coastal ecosystems.

Water temperature has been considered as a major factor controlling seasonal growth of seagrasses (Tutin 1942; Phillips *et al.* 1983; Lee and Dunton 1996; Lee *et al.* 2003). In the present study, both eelgrass productivity and water temperature exhibited distinct seasonal trends, but peaks of productivity and temperature occurred at different time. While eelgrass leaf productivity was highest in April and May, water temperature was highest in August. When all data were plotted, no strong correlation was apparent between leaf productivity and water temperature in this study (Fig. 8). The correlation between leaf production and temperature varied with season. Eelgrass leaf productivity increased with increasing water temperature during spring period, but decreased with increasing water temperature during summer. No

correlation has been observed between production and temperature during winter. Significant declines of eelgrass biomass and production have been reported at water temperature exceeded 30°C (Wetzel and Penhale 1983; Orth and Moore 1986; Marsh *et al.* 1986; Lee *et al.* 2003).

In the present study, leaf productivity reached a peak at water temperature of about 16-18°C, and then decreased with increasing water temperature. This pattern of the relationship between production and temperature probably resulted from rapid increases in eelgrass leaf respiration at high water temperature (Biebl and McRoy 1971; Drew 1979; Bulthuis 1983; Marsh *et al.* 1986). Relative growth rate may represent quality of leaf tissues for production. In this study, relative growth rate was highest in spring and lowest during high temperature periods. Additionally, plastochrone interval was shortest in spring and longest in summer. These results also suggest that eelgrass plants have optimal temperature for growth during spring, but have reduced growth rates due to the harmful effect of high water temperature. Seasonal growth dynamics of temperate seagrass, *Zostera marina* in this study area was mainly regulated by water temperature, and eelgrass leaf production significantly reduced at high water temperature exceeded 20°C.

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REFERENCES

- Biebl R. and McRoy C.P. 1971. Plasmatic resistance and rate of respiration and photosynthesis of *Zostera marina* at different salinities and temperatures. *Mar. Biol.* **8**: 48-56.
- Bulthuis D.A. 1983. Effects of temperature on the photosynthesis-irradiance curve of the Australian seagrass, *Heterozostera tasmanica*. *Mar. Biol. Lett.* **4**: 47-57.
- Cambridge M.L., Chiffings A.W., Moore B.L. and McComb A.J. 1986. The loss of seagrass in Cockburn Sound, Western Australia. II. Possible causes of seagrass decline. *Aquat. Bot.* **24**: 269-285.
- Cambridge M.L. and McComb A.J. 1984. The loss of seagrasses in Cockburn Sound, Western Australia. I. The time course and magnitude of seagrass decline in relation to industrial

- development. *Aquat. Bot.* **20**: 229-243.
- Chin-Leo G. and Benner R. 1991. Dynamics of bacterioplankton abundance and production in seagrass communities of a hypersaline lagoon. *Mar. Ecol. Prog. Ser.* **73**: 219-230.
- Czerny A.B. and Dunton K.H. 1995. The effects of in situ light reduction on the growth of two species of subtropical seagrasses, *Thalassia testudinum* and *Halodule wrightii*. *Estuaries* **18**: 418-427.
- Dennison W.C. 1987. Effects of light on seagrass photosynthesis, growth and depth distribution. *Aquat. Bot.* **27**: 15-26.
- Dennison W.C., Aller R.C. and Alberte R. 1987. Sediment ammonium availability and eelgrass (*Zostera marina*) growth. *Mar. Biol.* **94**: 469-477
- Dennison W.C., Orth R.J., Moore K.A., Stevenson J.C., Carter V., Kollar S., Bergstrom P.W. and Batiuk. R.A. 1993. Assessing water quality with submersed aquatic vegetation. *BioScience* **43**: 86-94.
- Drew E.A. 1979. Physiological aspects of primary production in seagrasses. *Aquat. Bot.* **7**: 139-150.
- Dunton K.H. 1990. Production ecology of *Ruppia maritima* L. s.l. and *Halodule wrightii* Aschers. in two subtropical estuaries. *J. Exp. Mar. Biol. Ecol.* **143**: 147-164.
- Dunton K.H. 1994. Seasonal growth and biomass of the subtropical seagrass *Halodule wrightii* in relation to continuous measurements of underwater irradiance. *Mar. Biol.* **120**: 479-489.
- Fonseca M.S. 1989. Sediment stabilization by *Halophila decipiens* in comparison to other seagrasses. *Estuarine Coast. Shelf Sci.* **29**: 501-507.
- Giesen W.B.J.T., van Katwijk M.M. and den Hartog C. 1990. Eelgrass condition and turbidity in the Dutch Wadden Sea. *Aquat. Bot.* **37**: 71-85.
- Harlin M.M. and Thorne-Miller B. 1981. Nutrient enrichment of seagrass beds in a Rhode Island coastal lagoon. *Mar. Biol.* **65**: 221-229.
- Heck K.L.Jr. and Westone G.S. 1977. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. *J. Biogeog.* **4**: 135-142.
- Huh S.H. and Kitting C.L. 1985. Trophic relationships among concentrated populations of small fishes in seagrass meadows. *J. Exp. Mar. Biol. Ecol.* **92**: 29-43.
- Iizumi H. and Hattori A. 1982. Growth and organic production of eelgrass (*Zostera marina* L.) in temperate waters of the Pacific coast of Japan. III. The kinetics of nitrogen uptake. *Aquat. Bot.* **12**: 245-256.
- Iizumi H., Hattori A. and McRoy C.P. 1982. Ammonium regeneration and assimilation in eelgrass (*Zostera marina*) beds. *Mar. Biol.* **66**: 59-65.
- Kentula M.E. and McIntire C.D. 1986. The autecology and production dynamics of eelgrass (*Zostera marina* L.) in Netarts bay, Oregon. *Estuaries* **9**: 188-199.
- Kenworthy W.J. and Thayer G.W. 1984. Production and decomposition of the roots and rhizomes of seagrasses, *Zostera marina* and *Thalassia testudinum*, in temperate and subtropical marine ecosystems. *Bull. Mar. Sci.* **35**: 364-379.
- Kenworthy W. J., Zieman J.C. and Thayer G.W. 1982. Evidence for the influence of seagrasses on the benthic nitrogen cycle in a coastal plain estuary near Beaufort, North Carolina (USA). *Oecologia* **54**: 152-158.
- Koepfler E.T., Benner R. and Montagna P.A. 1993. Variability of dissolved organic carbon in sediments of a seagrass bed and an unvegetated area within an estuary in southern Texas. *Estuaries* **16**: 391-404.
- Lee K.-S. and Dunton K.H. 1996. Production and carbon reserve dynamics of the seagrass *Thalassia testudinum* in Corpus Christi Bay, Texas, USA. *Mar. Ecol. Prog. Ser.* **143**: 201-210.
- Lee K.-S. and Dunton K.H. 1997. Effects of *in situ* light reduction on the maintenance, growth and partitioning of carbon resources in *Thalassia testudinum*. *J. Exp. Mar. Biol. Ecol.* **210**: 53-73.
- Lee K.-S. and Dunton K.H. 1999. Inorganic nitrogen acquisition in the seagrass *Thalassia testudinum*: Development of a whole-plant nitrogen budget. *Limnol. Oceanogr.* **44**: 1204-1215.
- Lee K.-S. and Dunton K.H. 2000. Effects of nitrogen enrichment on biomass allocation, growth, and leaf morphology of the seagrass *Thalassia testudinum*. *Mar. Ecol. Prog. Ser.* **196**: 39-48.
- Lee K.-S., Kang C.-K. and Kim Y.-S. 2003. Seasonal dynamics of the seagrass *Zostera marina* on the south coast of the Korean peninsula. *J. Korean Soc. Oceanogr.* **38**: 68-79.
- Mann K.H. 1988. Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. *Limnol. Oceanogr.* **33**: 910-930.
- Marsh J.A.Jr., Dennison W.C. and Alberte R.S. 1986. Effects of temperature on photosynthesis and respiration in eelgrass (*Zostera marina* L.). *J. Exp. Mar. Biol. Ecol.* **101**: 257-267.
- McRoy C.P. and McMillan C. 1997. Production ecology and physiology of seagrasses. In: McRoy C.P. and Helfferrich C. (eds), *Seagrass ecosystems: a scientific perspective*. Dekker, New York, pp. 53-81.
- Murray L., Dennison W.C. and Kemp W.M. 1992. Nitrogen versus phosphorus limitation for growth of an estuarine population of eelgrass (*Zostera marina*). *Aquat. Bot.* **44**: 83-100.
- Ogden J.C. 1980. Faunal relationships in Caribbean seagrass beds. In: Phillips R.C. and McRoy C.P. (eds), *Handbook of seagrass biology, an ecosystem perspective*. Garland STPM Press, New York. pp. 173-198.
- Onuf C.P. 1994. Seagrasses, dredging and light in Laguna Madre, Texas, U.S.A. *Estuarine Coast. Shelf Sci.* **39**: 75-91.
- Opsahl S. and Benner R. 1993. Decomposition of senescent blades of seagrass *Halodule wrightii* in a subtropical lagoon. *Mar. Ecol. Prog. Ser.* **94**: 191-205.
- Orth R.J. 1977. Effect of nutrient enrichment on growth of eelgrass *Zostera marina* in the Chesapeake Bay, Virginia, USA. *Mar. Biol.* **44**: 187-194
- Orth R.J., Heck K.L.Jr. and Montfrans J.V. 1984. Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries* **7**: 339-350.

- Orth R.J. and Moore K.A. 1983. Chesapeake Bay: An unprecedented decline in submerged aquatic vegetation. *Science* **222**: 51-53.
- Orth R.J. and Moore K.A. 1986. Seasonal and year-to-year variations in the growth of *Zostera marina* L. (eelgrass) in the lower Chesapeake Bay. *Aquat. Bot.* **24**: 335-341.
- Ott J.A. 1979. Persistence of a seasonal growth rhythm in *Posidonia oceanica* (L.) Delile under constant conditions of temperature and illumination. *Mar. Biol. Lett.* **1**: 99-104.
- Parsons T.R., Maita Y. and Lalli C.M. 1984. *A manual of chemical and biological methods for seawater analysis*. Pergamon Press, New York. 173pp.
- Pedersen M.F., Paling E.I. and Walker D.I. 1997. Nitrogen uptake and allocation in the seagrass *Amphibolis antarctica*. *Aquat. Bot.* **56**: 105-117.
- Peduzzi P. and Herndl G.J. 1991. Decomposition and significance of seagrass leaf litter *Cymodocea nodosa* for the microbial food web in coastal waters (Gulf of Trieste, Northern Adriatic Sea). *Mar. Ecol. Prog. Ser.* **71**: 163-174.
- Perez M., Romero J., Duarte C.M. and Sand-Jensen K. 1991. Phosphorus limitation of *Cymodocea nodosa* growth. *Mar. Biol.* **109**: 129-133.
- Phillips R.C., McMillan C. and Bridges K.W. 1983. Phenology of eelgrass, *Zostera marina* L., along latitudinal gradients on North America. *Aquat. Bot.* **15**: 145-146.
- Romero J., Perez M., Mateo M.A. and Sala E. 1994. The below-ground organs of the Mediterranean seagrass *Posidonia oceanica* as a biogeochemical sink. *Aquat. Bot.* **47**: 13-19.
- Short F.T. 1983. The seagrass, *Zostera marina* L.: Plant morphology and bed structure in relation to sediment ammonium in Izembek Lagoon, Alaska. *Aquat. Bot.* **16**: 149-161.
- Short F.T., Dennison W.C. and Capone D.G. 1990. Phosphorus-limited growth of the tropical seagrass *Syringodium filiforme* in carbonate sediments. *Mar. Ecol. Prog. Ser.* **62**: 169-174.
- Short F.T. and McRoy C.P. 1984. Nitrogen uptake by leaves and roots of the seagrass *Zostera marina* L. *Bot. Mar.* **27**: 547-555.
- Stapel J., Aarts T.L., van Duynhoven B.H.M., de Groot J.D., van den Hoogen P.H.V. and Hemminga M.A. 1996. Nutrient uptake by leaves and roots of the seagrass *Thalassia hemprichii* in the Spermonde Archipelago, Indonesia. *Mar. Ecol. Prog. Ser.* **134**: 195-206.
- Summerson H.C. and Peterson C.H. 1984. Role of predation in organizing benthic communities of a temperate-zone seagrass bed. *Mar. Ecol. Prog. Ser.* **15**: 63-77.
- Terrados J. and Williams S.L. 1997. Leaf versus root nitrogen uptake by the surfgrass *Phyllospadix torreyi*. *Mar. Ecol. Prog. Ser.* **149**: 267-277.
- Tutin T.G. 1942. *Zostera*. *J. Ecol.* **30**: 217-266.
- Vermaat J.E., Hootsmans M.J.M. and Nienhuis P.H. 1987. Seasonal dynamics and leaf growth of *Zostera noltii* Hornem., a perennial intertidal seagrass. *Aquat. Bot.* **28**: 287-299.
- Ward L.G., Kemp W.M. and Boynton W.R. 1984. The influence of waves and seagrass communities on suspended particulates in an estuarine embayment. *Mar. Geol.* **59**: 85-103.
- Wetzel R.G. and Penhale P.A. 1983. Production ecology of seagrass communities in the lower Chesapeake Bay. *Mar. Techn. Soc. J.* **17**: 22-31.
- Williams S.L. and Ruckelshaus M.H. 1993. Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and epiphytes. *Ecology* **74**: 904-918.
- Zieman J.C. 1974. Methods for the study of the growth and production of turtle grass, *Thalassia testudinum* Konig. *Aquaculture* **4**: 139-143.
- Zieman J.C. and Wetzel R.G. 1980. Productivity in seagrasses: methods and rates. In: Phillips R.C. and McRoy C.P. (eds), *Handbook of seagrass biology: an ecosystem perspective*. Garland STPM Press, New York. pp. 87-116.

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